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A COMPARISON OF SONG SYLLABLE PERCEPTION BY FIVE SPECIES OF BIRDS

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ABSTRACT: Perception of song syllables taken from natural song sparrow and swamp sparrow songs was examined in five different species: song sparrows (*Melospiza melodia*), swamp sparrows (*Melospiza georgiana*), zebra finches (*Taeniopygia guttata catanotis*), canaries (*Serinus canaria*), and budgerigars (*Melopsittacus undulatus*). Using operant conditioning techniques, we trained these birds to discriminate among sparrow song syllables. By testing the birds on all possible pair-wise combinations of syllables, we generated "similarity" matrices for these song syllables from the birds' response latencies to detect changes in a repeating background of syllables. A number of different statistical techniques were used to examine species differences in perception including factor analysis of an inter-species correlation matrix, cluster analysis of the similarity matrices, and individual-differences multidimensional scaling (MDS) of the similarity matrices from each species. The spatial map of these stimuli produced by MDS revealed the perceived relations among these syllables for each species. Several acoustic measurements taken from these syllables were correlated with stimulus coordinates of the syllables in multidimensional space. These results demonstrate that natural vocal signals can be effectively used as stimuli in psychoacoustic experiments and the outcome of such experiments are likely to reveal robust species differences in perception.

Much is known about song learning in two congeneric species of sparrow, the song sparrow (*Melospiza melodia*) and the swamp sparrow (*Melospiza georgiana*) (Marler & Peters, 1981; Marler, 1987). It is also known that these two species exhibit innate preferences for the learning of species-specific songs (Marler & Peters, 1977, 1989). But the boundary conditions of these innate preferences are likely complex. Male swamp sparrows, for instance, can learn song sparrow notes from hybrid syllables in which song sparrow notes are inserted in swamp sparrow syllables and presented in swamp sparrow temporal patterns (Marler, 1987).

Recent studies have begun to focus on perceptual processing in these two species (Marler & Peters, 1989). A perceptual predisposi-

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tion to learn conspecific song is most likely innate in swamp sparrows and perhaps also in song sparrows (Dooling & Searcy, 1980). Because they sing and defend their territories, male song birds have more often been the subject of studies on the responsiveness to natural, synthetic, and modified vocalizations. But using copulation solicitation displays, it has recently been shown that female song sparrows and female swamp sparrows were also sensitive to both species-specific phonology and temporal patterns (Searcy, Marler, & Peters, 1981).

We recently applied operant conditioning procedures to study basic auditory perception (Okanoya & Dooling, 1988a) and the perception of song syllables by both species of sparrow (Okanoya & Dooling, 1990). These two species of sparrow are slightly different in terms of absolute auditory sensitivity which parallels species differences in the long term average power spectra of the song (Okanoya & Dooling, 1988b). Furthermore, females of both species perceived the differences between normal and modified swamp sparrow and song sparrow syllables with swamp sparrows tending to be somewhat more discriminating than song sparrows (Okanoya & Dooling, 1990).

In the present experiments, we tested other species of small birds on these same syllables. By comparing the results of sparrows tested on sparrow syllables with other species tested on the same syllables, it is possible to arrive at an indication of whether the perception of song syllables by sparrows is in any way "special." If sparrows and other species of birds all perceive sparrow song syllables in a similar way, then we can conclude that the perceptual mechanisms used by sparrows in perceiving song syllables are not special but are probably due instead to general auditory-system processing mechanisms common to all birds.

METHOD

Animals

For this experiment we had available to us only female sparrows: two song sparrows and two swamp sparrows. The remaining birds were four budgerigars (*Melopsittacus undulatus*) (1 female and 3 males), two German Roller canaries (*Serinus canaria*) (1 male, 1 female), and four zebra finches (*Taeniopygia guttata (catanotis)*) (2 females, 2 males). The four sparrows reported here were the same birds tested previously (Okanoya & Dooling, 1990). These birds were hand-reared at the Rockefeller University Field Research Center in New York and were excluded, on the basis of their sex, from a study on song learning. The budgerigars, canaries, and finches were obtained from local commercial pet dealers or bred in the laboratory. During

the behavioral testing, the birds were housed in an aviary at the University of Maryland and maintained under a day/night cycle correlated with the season.

Apparatus

The apparatus used for training and testing the birds has been described previously (Okanoya & Dooling, 1988a, 1990). The birds were tested in a small wire cage ($15 \times 15 \times 15$ cm) placed in a sound attenuation chamber (IAC-1: $39 \times 58 \times 35$ cm). A standard pigeon grain hopper was mounted on one side of the cage. A response panel consisting of two sensitive microswitches with attached light emitting diodes (LEDs) was mounted just above the hopper opening. The birds could close the microswitch by striking the LED with their beaks.

All experimental events including stimulus presentation, response measurement, and reinforcement contingencies were controlled by an IBM-AT microcomputer. The song syllables were stored on the hard disk of the computer in digital form, output at a sampling rate of 20 kHz through a digital-to-analog converter (Data-translation DT2801A) and low-pass filtered at 10 kHz for anti-aliasing. A loud speaker mounted inside the sound proof chamber transduced the stimuli. Song syllables were presented at a peak sound pressure level of 72 dB(A) SPL at the bird's head as measured by a General Radio 1982 sound level meter.

Stimuli

The song syllables used in this experiment were taken from original field recordings of full length songs of both species made by Dr. Donald Kroodsma while he was at the Rockefeller University. Songs of swamp sparrows typically consist of a repetition of a single syllable whereas the songs of song sparrows are more complex, consisting of 3 to 6 different syllables arranged in a characteristic syntactical pattern (Marler & Peters, 1989). Since swamp sparrow songs consist of simple repetition of a single syllable, we selected syllables from song sparrow songs which occurred in the repetitive sections of the song.

In all, ten song syllables of roughly equal length (100-160 ms) were selected from both song and swamp sparrow songs. These syllables are shown in Figure 1 and are the same set used to test the sparrows in an earlier paper (Okanoya & Dooling, 1990). We did not conduct an exhaustive acoustic analyses of these syllables. But, a total of 32 acoustic measures were taken from these syllables for the purpose of finding a correlation between the acoustic characteristics of these complex stimuli and species differences in perception. In addition to duration, bandwidth, lowest frequency, highest frequency,

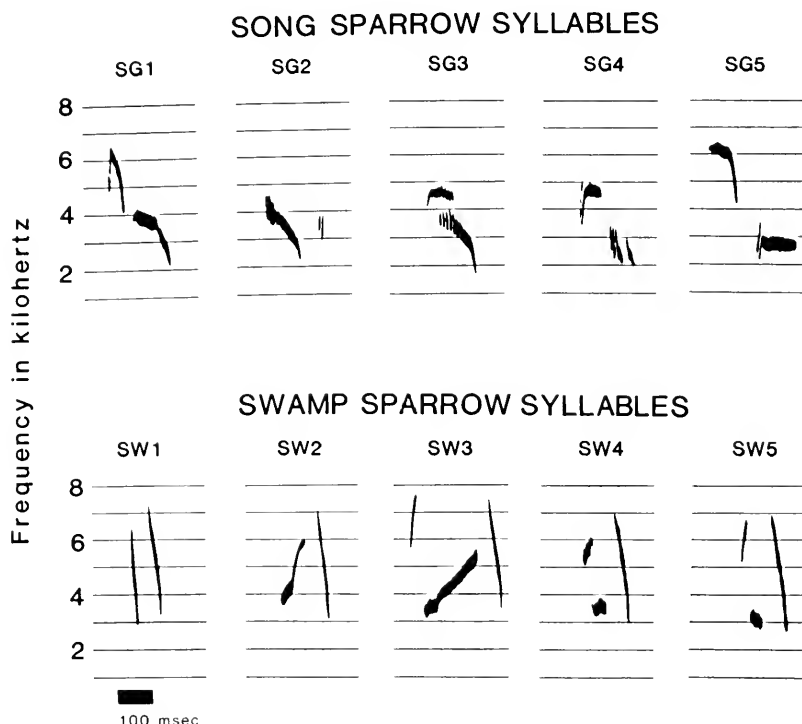


FIGURE 1. Sonograms of the set of natural song sparrow and swamp sparrow syllables used in this experiment.

and peak frequency, we also measured a number of additional spectral measures. We computed the long term average power spectrum over the entire duration of each syllable using ILS-PC. Then, we examined the distribution of energy in these syllables in selected bands from 1.0 kHz to 10.0 kHz and expressed the result as a percent relative to the total energy in the syllable (e.g., percentage of energy in the 1-2 kHz band).

Training and Testing Procedure

The training and testing procedures used in these experiments have also been described in detail elsewhere (Okanoya & Dooling, 1988a, 1988c, 1990) and thus are only briefly summarized here. Birds were food deprived overnight and for several hours in the morning. These birds were trained to peck one key (observation key) repeatedly during the repetitive presentation of one syllable (background) and to

peck the other key (report key) when another syllable (the target) was presented instead of the background. Syllables were presented at a rate of 5 per s to mimic the temporal pattern of swamp sparrow songs. A peck on the report key during a change in the repeating syllable was reinforced by access to food. Once the birds learned this response, they were tested on the set of syllables consisting of five song sparrow syllables and five swamp sparrow syllables (Figure 1).

A habituation phase preceded each testing phase. During this phase neither keylight was illuminated and the background sound was repeated until the bird either pecked the observation key four times or refrained from responding on the report key for 10s. Once either of these conditions was met, the LEDs on both observation and report keys were illuminated and the testing phase began. This procedure was highly effective in decreasing spontaneous responding.

During the test phase, a peck on the observation key initiated a random waiting interval of 1-7 s. Following this interval, a peck on the observation key resulted in the replacement of the background repeating syllable with the target syllable. A response to the report key within 3s from the beginning of the repeating target stimuli was reinforced with a 2s (budgerigars) to 4s (other species) access to food. About 20% of the trials were sham trials in which the target stimulus was the same as background stimulus. A response on the report key during a sham trial or during a waiting interval was punished with a 16s timeout period during which lights in the test chamber were extinguished but the repeating sound continued.

The testing phase continued until the background stimulus was paired with every other stimulus in the set three times. Testing proceeded a row at a time (i.e., same background stimulus) until all possible combinations within the row were exhausted. Following a 10s silent interval, another background stimulus was then randomly selected and a new habituation phase begun. This was continued until all stimuli had served as a background and as a target. This procedure produced a total of three latency matrices for analysis.

A median reaction time matrix was constructed out of the three latency matrices. The response latency required to detect changes in the repeating background syllable was taken as an index of perceptual similarity between the background and the target syllables (Okanoya & Dooling, 1988b). The upper and lower triangular halves of the matrix were averaged and log-transformed and the diagonal discarded to produce a single half-matrix of response latencies for each bird. For some of the following analyses, the half-matrices for the individuals of each species were then averaged to produce a single half-matrix for each species. An example of such a log-transformed half-matrix is given in Table 1.

TABLE 1
Response Latency Half-Matrix for Swamp Sparrows
(Log \times 100)

SG1	X									
SG2	312	X								
SG3	302	322	X							
SG4	306	300	306	X						
SG5	304	307	297	300	X					
SW1	302	297	299	301	305	X				
SW2	311	302	296	304	287	311	X			
SW3	306	315	301	295	299	313	328	X		
SW4	303	296	301	295	293	310	311	318	X	
SW5	303	300	292	298	289	308	312	301	315	X
	SG1	SG2	SG3	SG4	SG5	SW1	SW2	SW3	SW4	SW5

Statistical Procedures

Four procedures were used to assess the differences among species in the perception of sparrow syllables. First, the log-transformed half-matrices for each bird were used to construct a matrix of interindividual correlations. Principal components (Varimax rotation of all components) were computed for this matrix using SYSTAT. The purpose of this analysis was simply to provide a visual representation of the similarity in response patterns (i.e., between half-matrices) among individuals and among species. The spatial arrangement of the individual birds on the two highest rotated loadings in two-component space provides one way of characterizing the differences in response patterns among individuals.

Another way of characterizing differences in response latency matrices is through cluster analyses. To this end, a single half-matrix for each species was obtained by averaging the half-matrices of individual members of the species. Each average half-matrix was then submitted to a hierarchical, complete linkage, cluster analysis (Aldenderfer & Blashfield, 1984). The results of these cluster analyses indicate the extent to which each species perceived the differences between swamp and song sparrow syllables and the similarity among sparrow syllables from the same species.

In a third procedure, the half-matrices for each species were analyzed by a multidimensional scaling analysis (MDS) program, SIND-

SCAL (Shepard, 1980). MDS arranges stimuli in multidimensional space so that stimulus similarity (as determined by response latencies) is represented by spatial proximity. Species weights provide an indication of how well the arrangement of syllables in multidimensional space accounts for the data from each species.

Finally, a fourth procedure was used in conjunction with the multidimensional scaling analysis described above. In all, we measured 32 spectral, temporal, and intensive acoustic measures from these sparrow syllables. These measures were then correlated with the stimulus coordinates from MDS. To the extent that these measures were significantly correlated with syllable location in multidimensional space, they provide a potential explanation of the stimulus map in acoustic terms.

RESULTS

The two-component solution from the intercorrelation of the 14 matrices is shown in Figure 2. An interesting pattern emerges from

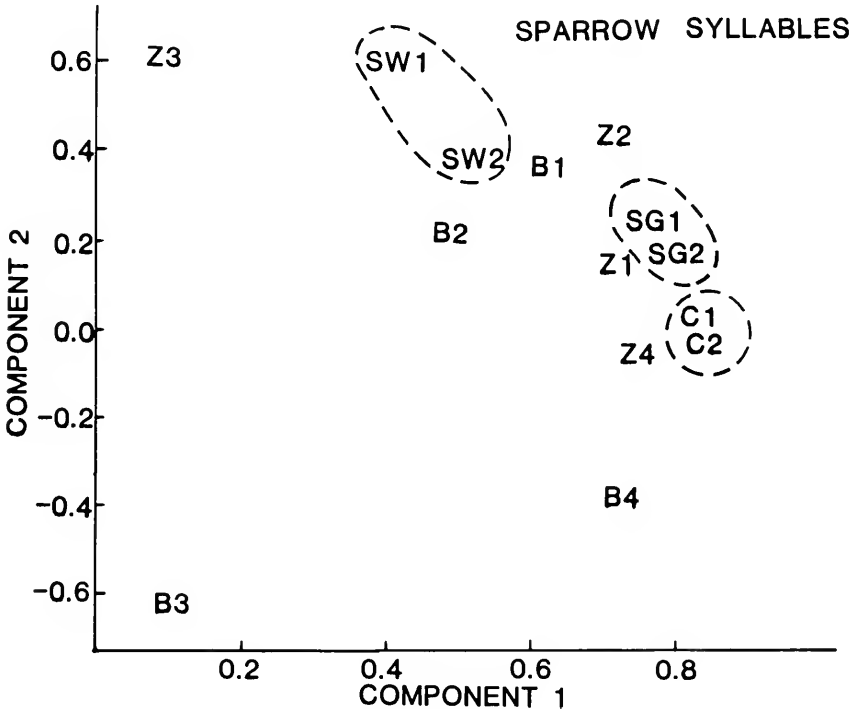


FIGURE 2. Two-dimensional Principle Component Analysis of the interindividual correlation matrix. All four sparrows as well as C1, B1, Z1, Z2 are females. Birds B2, B3, C2, Z3 and Z4 are males.

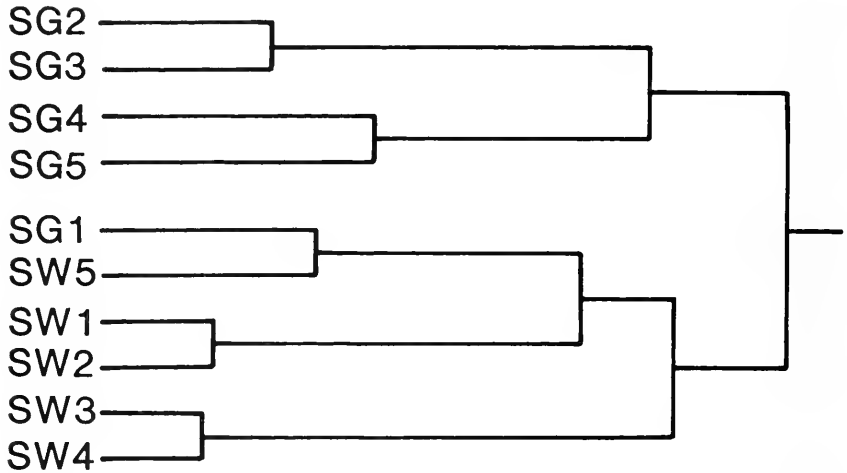


FIGURE 3. Cluster dendrograms of the summed response latency matrix from the five species.

this analysis. First, while there are clear species differences among canaries, song sparrows, and swamp sparrows, there are relatively small individual differences within each of these species—the differences among individuals of the same species are quite small compared to the differences among individual budgerigars and zebra finches.

Dendrograms from the cluster analyses of the data from all species combined showed that these 10 syllables were clustered into two groups corresponding fairly well to the species of sparrow. One of the song sparrow syllables is in among the cluster of swamp sparrow syllables. These results are shown in Figure 3. Separate cluster analyses were also performed on the data from each species. These analyses revealed that only swamp sparrows clearly showed two major clusters of syllables corresponding to the species of sparrow which produced them. Song sparrows intermixed only one syllable of each type. Dendrograms from all the other species showed somewhat more of an intermixing of swamp and song sparrow syllables.

The two-dimensional spatial representation obtained by a SINDSCAL analysis of the response latencies matrices of each species is shown in Figure 4a. The variance accounted for by this two-dimensional solution was 55% with the first and second dimensions accounting for 33% and 22%, respectively. The species weights (i.e., one weight for each species) for this solution are shown in Figure 4b.

In two-dimensional stimulus space, the 10 sparrow syllables are separated roughly into two groups by species along the first dimension. This arrangement follows closely the grouping that was evident from a cluster analysis on the data from all five species (Figure 3).

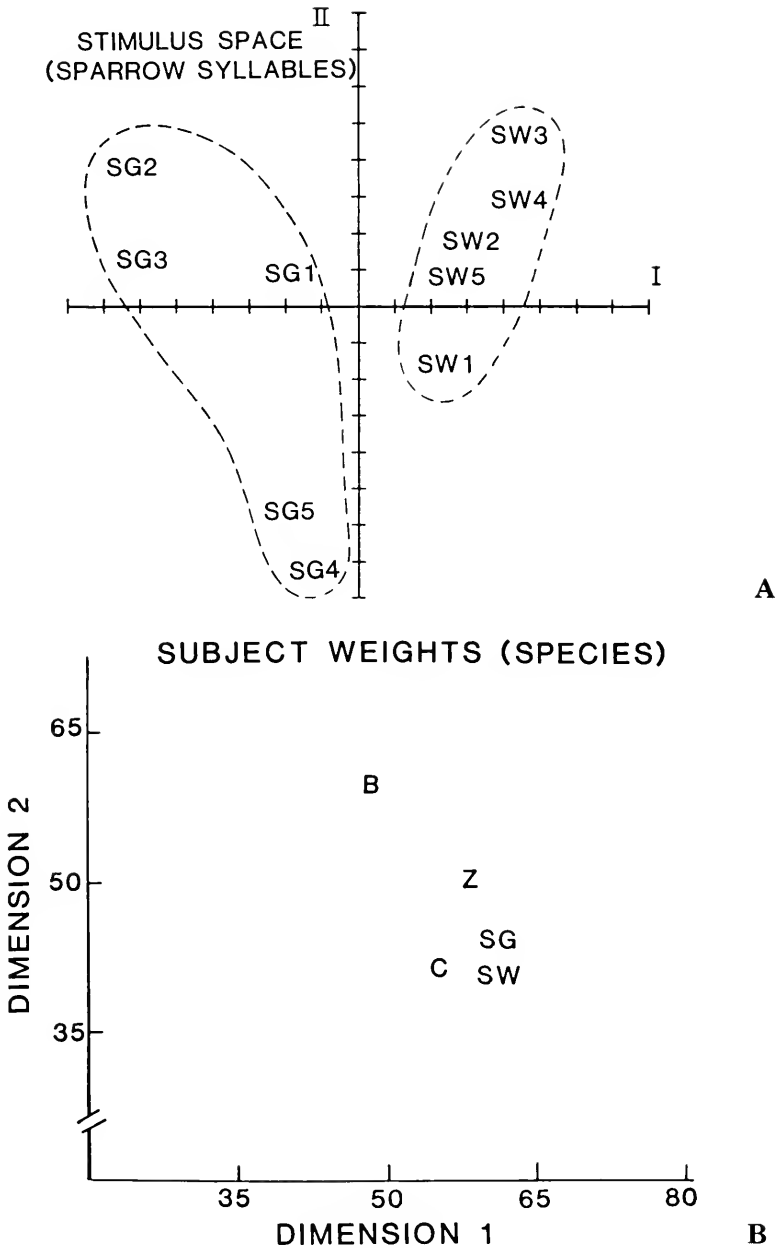


FIGURE 4 (a). Two-dimensional spatial representation of the eight sparrow syllables by the five species. Swamp sparrow syllables are on the left and song sparrow syllables are on the right. **(b)** Species weights corresponding to this stimulus space for the five species—budgerigars(B), canaries(C), zebra finches(Z), swamp sparrows(SW), and song sparrows(SG).

The relation among the species weights for this solution reflects the relative amount of variance in each species' data that is accounted for by the distances between stimuli in the spatial map. The species weights for song and swamp sparrows are very similar. Furthermore, the first dimension of the stimulus space accounts for more variance in the two sparrows' data than for the other three species. It is this dimension that separates the 10 syllable types by species. The second dimension accounts for more variance in the data of budgerigars and zebra finches than for the other three species. The characteristics of the stimuli represented by this dimension are less obvious from visual inspection alone.

Correlation between Syllable Coordinates in Perceptual Space and Acoustic Measures

In an effort to explain the stimulus space in acoustic terms, we measured a total of 32 acoustic characteristics of these syllables. This was not intended to be an exhaustive analysis. Rather, we selected measures which made sense from examination of sonographs of these syllables and which other investigators have used to characterize the differences between swamp and song sparrow songs (Marler & Pickert, 1984). These characteristics ranged from note durations, duration and direction of frequency sweeps, inter-note durations, and syllable durations to a variety of spectral measures including total energy in selected bandwidths. Many of these measures are also correlated to some degree with one another (e.g., syllable duration and internote-intervals).

We correlated these acoustic characteristics with location of stimuli in multidimensional space. Of these 32 measures, only five were correlated with stimulus coordinates on either the first or second dimension and all of these were spectral measures. Four measures were significantly correlated with stimulus coordinates along the first dimension. One is the total amount of energy in the region of 2-4 kHz and the other three are related to the bandwidth of these syllables (i.e., bandwidth, the lowest frequency, and the highest frequency). Only one measure, the amount of energy in the region of 2-3 kHz, was significantly correlated with stimulus coordinates along the second dimension. Some temporal measures such as syllable duration, inter-note-intervals, and percent of constant frequency portions of the syllables (the inverse of percent of sweep portions) are notable for their lack of correlation with the stimulus coordinates in perceptual space. These results are given in Table 2.

DISCUSSION

Most of what we know about the perceptual basis of selective vocal learning in sparrows comes from song learning experiments of

TABLE 2
Correlation Coefficients of Acoustic Properties with Stimulus Coordinates

<i>Property</i>	<i>Dimension I</i>	<i>Dimension II</i>
Bandwidth	0.670*	-0.183
High Frequency	0.884**	0.144
Low Frequency	0.801**	0.495
Energy 2-4kHz	-0.822**	0.132
Energy 2-3kHz	-0.429	-0.810**
Syllable Duration	-0.106	0.035
Internote-interval	0.221	0.235
Percent CF	0.256	0.561

**p*<.05

***p*<.01

Marler and his colleagues (Marler & Peters, 1989). Field playback studies with male sparrows (Peters, Searcy, & Marler, 1980), copulation/solicitation studies with female sparrows (Searcy et al., 1981), and heart rate recordings (Dooling & Searcy, 1980) have also been quite useful in refining the understanding of perceptual selectivity for conspecific song in these sparrows. Still, none of these measures have addressed the issue of whether swamp and song sparrows perceive their song syllables differently than any other avian species might perceive them. In other words, the issue of whether sparrows might be specialized for the perception of conspecific song syllables has not been explored. The present experiments describe an approach that might be useful in answering this question and, by comparing perception of song syllables in swamp and song sparrows and three other species of small birds, provides some preliminary evidence.

The results of these experiments show that sparrows emerge as different from these other species in the perception of sparrow syllables. First, the results of a Principle Components analysis on the intercorrelation matrix of all 14 birds revealed that both species of sparrows are similar to one another and to canaries in the consistency with which individual birds perceived the differences among the 10 sparrow syllables. This is in contrast to the results of both zebra finches and budgerigars who showed large interindividual differences. Perhaps this difference is related to the fact that complex, stereotyped, tonal syllables are a common feature of canary (Güttinger, 1985), swamp sparrow, and song sparrow song. Simple tonal syllables are a less common feature of the long rambling budgerigar song and do not occur at all in zebra finch song (Farabaugh, Brown & Dooling, submitted; Immelmann, 1969).

Reasoning along these same lines, the syllables in this experi-

ment were presented in a fixed temporal pattern approximating that found in normal swamp sparrow song. This patterning also bears some resemblance to normal canary song and to subunits of normal song sparrow song. Budgerigars and zebra finches, on the other hand, have a considerably different arrangement in the temporal pattern of their songs.

Thus, temporal patterning in the presentation of these syllables could have a differential effect on the perception of these syllables by the five species. However, the suggestion that sparrows and canaries may have more in common in the perception of these syllables than do the other species must be tempered by the small sample size. A proper test of this hypothesis would require testing many more sparrows and extending these tests to both males and females of each species.

The results of cluster analyses on the data for each bird revealed that only swamp sparrows showed two complete clusters of syllables corresponding perfectly to species type. These results support a variety of earlier studies showing that swamp sparrows are more selective than song sparrows in the perception of conspecific syllables (Dooling & Searcy, 1980; Marler, 1987; Okanoya & Dooling, 1990). The four other species tested in this experiment all showed a slight intermixing of swamp and song sparrow syllables by a cluster analysis.

The results of multidimensional scaling and property fitting are interesting for what they reveal about the relative sensitivities of the five species. The species weights of both sparrow species are highest on the first dimension—the dimension that separates song sparrow syllables from swamp sparrow syllables. We take this as evidence that, compared to the other three species, swamp and song sparrows are more sensitive to the acoustic differences between swamp and song sparrow syllables.

An obvious feature of these syllables that would reliably discriminate between the two classes of syllables is the broad spectrum, rapid frequency glide (Type VI Note) present in all swamp sparrow syllables (Marler & Pickert, 1984). Not surprisingly, this feature also contributes heavily to the quantitative acoustic measures of bandwidth, low frequency limit, and high frequency limit in swamp sparrow syllables. It is perhaps not surprising then that these three measures are significantly correlated with stimulus coordinates along the first dimension in multidimensional space. We conclude that this feature probably discriminates most reliably between the syllables of the two species, and that both swamp sparrows and song sparrows are most sensitive to this feature.

The preponderance of energy in these syllables falls in the spectral region of 2-4 kHz. This is generally more true for song sparrow

syllables than swamp sparrow syllables. Again, it is not too surprising that this spectral measure is also significantly correlated with stimulus coordinates on the first dimension.

On the second dimension, the species weight for budgerigars is the highest followed by zebra finches, and then the two sparrow species and the canaries. From other psychoacoustic tests, we know that budgerigars are unusually sensitive to spectral changes in the frequency region around 3 kHz. The amount of energy in the spectral region of 2-3 kHz is correlated with syllable location on the second dimension in stimulus space. It is more difficult to account for differences among the other species on the second dimension because all four species show a similar pattern of spectral resolving power over the frequency range of about 1-5 kHz (Okanoya & Dooling, 1987).

Comparing the absolute auditory sensitivity of these species at high frequencies reveals another potential mechanism for the species differences in perception we observed. Swamp sparrows and song sparrows are 10-15 dB more sensitive to frequencies above 4 kHz than are canaries and zebra finches and 15-20 dB more sensitive than budgerigars (Okanoya & Dooling, 1987). The greater sensitivity of sparrows to high frequencies could contribute to the fact that sparrows, compared to the other species tested, are most sensitive to the differences between the two classes of sparrow syllables. This argument also supports the notion that the rapid, broad, frequency swept Type VI Note provides an important cue for distinguishing among the two classes of syllables.

The final explanation for the species differences observed in this experiment—including firm evidence for differential sensitivity to different song syllable features—will have to come from experiments with synthetic stimuli. The present experiment shows there are species differences in the perception of sparrow syllables and suggests a possible basis for these differences related to differences in basic auditory processes. But, it is likely that other perceptual and attentional factors residing at more central levels are also responsible. A similar conclusion was reached from a recent study comparing budgerigars, canaries, and zebra finches on the perception of conspecific and heterospecific distance calls (Dooling, Brown, Klump, & Okanoya, in press).

Whatever the final mechanism(s) turn out to be, one great advantage of the present procedures in pursuing the issue of species-specificity in song perception is that they can be used with equal facility not only on different species but also on males and females of the same species. Previous attempts to compare male and female perception of songs and song elements have had to rely on dramatically different methodologies for the two sexes. We feel this represents a considerable advance in the study of the perception of songs and song

syllables in birds. Comparing males and females of the same species should prove extremely interesting in species in which only the male sings and for which there is evidence of a motor basis for song perception.

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EFFECTS OF DIFFERENTIALLY REINFORCED PRE-EXPOSURE ON SIMULTANEOUS ODOUR DISCRIMINATION LEARNING IN THE ALBINO AND PIGMENTED RAT (*Rattus norvegicus*)

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ABSTRACT: Pigmented dark agouti and albino Wistar rats were compared for the effect of differentially reinforced pre-exposure to peppermint as a positive and vanilla as a negative odour cue. Both types of rat showed significantly enhanced performance on the simultaneous odour discrimination task with the same cues, when compared to control groups not pre-exposed to the odour cues. However, the pigmented rats had steeper learning curves than the albinos, with the albino controls performing significantly worse than the other groups. The results are discussed in terms of task components of cue significance and response regulation. It appeared that the response component was more difficult for the albino rats compared to the pigmented rats.

In this experiment pigmented and albino rats were compared for the efficacy of differentially reinforced pre-exposure to odour cues, in enhancing subsequent learning of a simultaneous odour discrimination task. In earlier studies we showed that differentially reinforced pre-exposure to three dimensional shapes (a triangle and a circle), in which one of the two cues was associated with food, significantly enhanced performance in a subsequent simultaneous discrimination learning task with the same or similar cues (Bell & Livesey, 1977, 1981). Pigmented (dark agouti) rats showed significantly greater transfer from the visual-tactual prior exposure than did albino rats even though there was no significant difference between them in the control condition (where no prior exposure had occurred). We demonstrated that the albino rats did not learn as much about the shape cue during prior exposure as did the pigmented rats and we attributed this to a difference in salience of the exposure stimuli for albino and pigmented animals in this situation (Bell & Livesey, 1981).

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Lubow, Rifkin, and Alek (1976) suggested that pre-exposure may be more effective with odour cues since it employs a more dominant sensory modality for the rat. The rat has a complex nasal cavity with intricate convolutions and large sorptive surface area, ideally suited to analysis of odorants. Behaviourally, a sniffing strategy is used which appears to be applied for effective detection, discrimination and recognition of odours (Youngentob, Mozell, Sheehe, & Hornung, 1987). Rats have been shown to attend to odour cues in preference to auditory or visual cues (Nigrosh, Slotnick, & Nevin, 1975); to show rapid learning of a go/no go discrimination with odour cues (Eichenbaum, Shedlack, & Eckmann, 1980) and learning-set performance with odour cues far superior to that with visual cues (Jennings & Keefer, 1969; Slotnick & Katz, 1974). According to Jennings & Keefer (1969), variety of rat (pigmented vs. albino) was not a significant factor in learning various odour discriminations which included peppermint and vanilla cues.

Most studies of odour pre-exposure have used nonreinforced exposure, exploring the effects of preference for odour (Cornwell, 1976) or adaptation to odours (Laing & Panhuber, 1980). No study previous to the present one has examined the effect of reinforced prior exposure to odour cues on subsequent discrimination performance. Lubow, et al.'s (1976) experiment investigated the effect of 14 days of nonreinforced pre-exposure to odour cues on discrimination performance with the same or other cues. In that study pre-exposure was for 2 hours daily, either to lemon versus water cues (presented at two outlets in the cage), or wintergreen versus water. The discrimination task was in a Y-maze with approach to the strong odour (lemon or wintergreen) reinforced with a food pellet and approach to water nonreinforced. Findings from the experiment included enhancement of discrimination learning with the same cues if pre-exposure was given in a different environment to the test environment. If, however, the pre-exposure and test environments were the same, discrimination learning appeared to be retarded. These findings are similar to our results from pre-exposure to non-differentially reinforced shape cues, where discrimination learning was enhanced only if pre-exposure and discrimination tasks were presented in different environments. However, with differentially reinforced pre-exposure, we found that discrimination learning was enhanced only if the pre-exposure and test environments were similar (Bell & Livesey, 1981).

In order to compare our odour discrimination results with those from the earlier shape discrimination experiments we used essentially the same apparatus and procedures as those employed in our earlier studies, rather than those that have been employed in other studies of odour discrimination learning. Previous tasks involved a simple approach response to the positive stimulus (Braun & Marcus, 1969; Eichenbaum et al., 1980; Kimble & Zack, 1967; Lubow et al.,

1976; O'Grady & Jennings, 1972; Ruddy, 1980; Slotnick & Nigrosh, 1974; Staubli, Fraser, Farraday, & Lynch, 1987). For our odour task the discriminanda were presented in a Grice-type manual apparatus with the stimuli mounted side by side on two panels, as described in Bell & Livesey (1981, 1988) for the visual/tactual tasks.

For presentation of the odour cues a gauze pad (5×5 cm) was taped to the middle of each stimulus panel and the odours were instilled into these pads. The rat had to push open the positive stimulus panel to retrieve the food reward, a small pellet of dog food presented from behind it. Since this apparatus and procedure had not previously been used for odour discrimination, preliminary studies were used to determine appropriate odour stimuli. Initially, lemon and water odours as used by Lubow et al. (1976) were investigated. However, these proved to be unsatisfactory in the discrimination apparatus. Both albino and pigmented rats showed an aversion for the lemon stimulus (not noted in previous reports), and performance was erratic in some animals. An alternative discrimination task, between peppermint and vanilla was tried, as this had been used previously with no reported problems or indication of possible preference or aversion for either odour (Jennings & Keefer, 1969; Kimble & Zack, 1967). Two groups of 6 brown rats each, were employed, one group trained with vanilla as the positive and peppermint as the negative stimuli and the other group with peppermint positive and vanilla negative.

This experiment revealed a clear preference for the vanilla positive condition evidenced by a significantly better performance by the vanilla positive group at all stages of acquisition. This effect was probably due to some aversion to the peppermint since the six drops of this essence used, produced a pungent and powerful odour. The need for the animal to approach close to the source of the odour in order to push the panel could have enhanced this aversion. It was also noted that the performance of individual rats was less erratic than in the lemon/water task. With such a pronounced preference for the vanilla cue, reinforced pre-exposure could have little additional effect on the performance of this task. We, therefore, decided that a peppermint-positive/vanilla-negative task would be suitable for the pre-exposure experiment, provided the strength of the vanilla and peppermint cues was reduced to reduce the aversion to peppermint.

Thus, with odour cues, pre-exposure was expected to be more effective for the albino rats since this involves a more dominant sense. We, therefore, decided to investigate the effect of differentially reinforced pre-exposure to odour cues on learning of an odour discrimination task presented in the same environment and comparing albino and pigmented rats. We predicted that an effective enhancement of discrimination learning would follow differentially reinforced pre-exposure in the albino group as well as in the pigmented group.

METHOD

The design of the experiment was a two by two factorial: Pre-exposure Condition (Control vs. Differentially Reinforced) by rat type (Brown vs. Albino). Planned comparisons, to test whether each of the two differentially reinforced (DR) groups performed significantly better than their respective control groups, were made using one-tailed *t* tests for the measure of number of trials to criterion. An unweighted means analysis of variance (because of uneven group numbers) was used to compare the rat types on this measure (Kirk, 1968). Rate of acquisition in terms of mean correct responses per day was examined by a Rat Types \times Conditions \times Days analysis of variance.

Animals

Eighteen male agouti rats (*Rattus norvegicus*, DA strain) from the colony bred within the Psychology Department and 18 male albino (Wistar strain) rats from the Biological Sciences Breeding unit, University of Western Australia were employed in the study. Animals were aged between 65-75 days at the beginning of the experiment. Housing consisted of racked cages (36 \times 26 \times 20 cm) with wire mesh back and front and solid metal sides. Rats were housed two or three from the same group per cage. The housing room was air conditioned (constant 22°C) with a 12 hr light/dark cycle.

Apparatus

This was essentially the same as that used in our shape discrimination experiments (Bell & Livesey, 1981).

Exposure Apparatus. There were six units, each consisting of a small mesh cage (36 \times 26 \times 20 cm) joined along one of the longer sides to a wooden compartment (25 \times 26 \times 20 cm) painted flat grey. The compartments could be separated by a metal slide. A clear Plexiglas lid was hinged over each compartment. In the end of the wooden compartment opposite the cage section, were two openings, 9 \times 9 cm and 4.5 cm apart. Behind the openings was a 9 cm projecting ledge on which two food containers could be placed so that one was behind each opening. Each container had a small tray at the bottom that was the only access to the food. The front of each container, including the food tray, was covered by an aluminium panel (14 \times 7.5 cm) that rats pushed inwards to reach the food. The food was a minced, concentrated dog food, preferred by the rats to the standard laboratory pellets. Cod liver oil was mixed with the food to provide a vitamin supplement. For the presentation of the odour cues the food container panels were covered with white opaque plastic. A dark gauze pad,

5 × 5 cm, was taped to the middle of the panel with the bottom of the pad 2 cm from the bottom. For the control groups two drops of water were placed on the food container panels, for the DR groups in pre-exposure the container without food had two drops of vanilla essence placed on the gauze pad. The container with the food in it had two drops of peppermint essence placed on the pad. The essences used were pure Fauldings food essences.

Test Apparatus. The two compartments were identical to those of the exposure apparatus but, instead of food containers, there were two small food wells behind the openings in the discrimination apparatus. Aluminium panels (16 × 10 cm) covered with white plastic were hung on a metal rod behind the openings. A gauze pad was taped to each panel. Two drops of vanilla essence were placed on one pad and two drops of peppermint were placed on the other. The panels were held closed against the back of the opening by magnetic tape. A gray wooden shield could be lowered in front of the stimuli. Reinforcement was obtained by pushing the entire stimulus panel backward exposing the food well. The incorrect response panel was held shut by a small wooden block placed behind it. When the incorrect panel was pushed partially open a microswitch on the block was closed and this activated a light outside the compartment signalling an error to the experimenter.

Procedure

Pre-exposure. Rats were handled by being placed on a tray, stroked and picked up for 20-min each day, placed on 22 hour food deprivation and introduced to dog food for 4-5 days prior to starting pre-exposure. All rats were given two 40-min feeding periods in the exposure apparatus, one in the morning and the other in the afternoon. During the 15 days of pre-exposure this was their only access to food. Water was available ad lib. The animals were fed singly in the exposure apparatus. At the beginning of the exposure period the rat was placed in the cage section, then the dividing shield was raised to allow access to the whole apparatus. To counteract association of food with a particular position, positions of the food containers were altered twice each period according to Fellows' (1967) revised Gellerman sequence. These changes were made at the beginning of the session and again halfway through. At that stage the rat was returned to the cage section with the slide inserted. It was then allowed re-entry when the container positions had been adjusted according to the sequence. Between exposure periods the food containers were removed and the air exhausted. For the first two days the panels on the food containers were taped open to accustom the rats to feeding from the containers.

For the 9 rats in each control group (Wistar and DA) pre-exposure was to containers (one with food, one empty) with no distinctive odour (water). For the 9 rats in each differentially reinforced (DR-Wistar and DR-DA) group, pre-exposure was to the peppermint scented panel on the container with food and the vanilla scented panel on the empty container. All animals were trained on the discrimination task with peppermint as the positive and vanilla as the negative cue.

On completion of the 15 days pre-exposure the rats were maintained on the 22 hour food deprivation schedule and discrimination training commenced. Pre-exposure was discontinued when testing began.

Discrimination Training. All rats were given 10 trials per day on the peppermint/vanilla discrimination. A noncorrection procedure was used. A response (push) to the negative stimulus panel signalled the end of the trial, the shield was lowered and the rat returned to the starting compartment. For a response to the positive stimulus panel, the rat pushed the panel fully open. The food pellet, made from the minced dog food was then presented to the animal on the end of a rod by the experimenter, so that the smell of the food did not interact with the odor stimuli. The food pellets were stored well away from the apparatus.

The positions of the two stimuli were determined for each trial by the Fellows sequence. The criterion for learning of the discrimination was 90% correct responses on three consecutive days. Rats had to complete the criterion trials with both stimulus panels unblocked to ensure that they were not using any extraneous cues that might have been provided by the block, e.g., pressure cues. Testing was conducted by the two experimenters. Between the end of the test session for one rat and the beginning for the next the stimulus panels were removed from the apparatus and the air exhausted for several minutes.

RESULTS

Results were considered for two measures: trials to criterion, that is, a broad measure of ability to learn the task; and rate of acquisition, measured by number of correct responses out of the 10 attempted each day.

Trials to Criterion

Using this measure, the principle hypothesis that differentially reinforced pre-exposure to the cues would result in significant improvement in acquisition of the discrimination task was tested using

TABLE 1
Mean Number of Trials to Criterion, with Standard Errors for Each Group

	CDA	CW	DRDA	DRW
Mean	82.2	117.5	67.7	80
Standard Error	4.93	13.72	4.93	8.65

Note: CDA = Control Dark Agouti. CW = Control Wistar. DRDA = Differentially Reinforced Dark Agouti. DRW = Differentially Reinforced Wistar.

the planned comparisons. Two animals, one from each of the albino groups, failed to reach criterion. These two animals, therefore, could not be included in the criterion analyses as they did not have trials to criterion measures. Mean trials to criterion for all the other rats in the four groups are shown in Table 1.

For both the albino Wistar and pigmented DA rats, performance of the DR group was significantly superior to the C group as assessed by one-tailed *t* tests (CDA VS DRDA, $t(16)=2.16$, $p = .025$; CW VS. DRW, $t(16)=2.24$, $p < .025$). Analysis of variance was by unweighted means because of loss of the two albino rats that did not reach criterion. This revealed that differences in both Rat Type ($F(1,30) = 9.6$, $p<.01$) and Condition ($F(1,30) = 8.06$, $p < .01$) were significant with a nonsignificant interaction. This analysis confirmed that for both W and DA rats, the differentially reinforced exposure significantly enhanced learning (nonsignificant interaction). Overall, the pigmented DA rats reached criterion in significantly fewer trials than the albino (W) rats, as shown in Table 1.

Rate of Acquisition

Figure 1 shows performance for each of the four groups in terms of mean correct responses per day. All 9 animals from each group were included in this analysis as failure to reach criterion did not affect this measure. All 18 of the brown rats and 10 of the 18 albinos had reached criterion by 10 days so this was taken as a cut off point for this analysis. Animals that had reached criterion before 10 days were given a score "10" for each subsequent day to Day 10.

These data were examined by a Rat Type (Wistar vs. DA) \times Condition (control vs. exposure) \times Days analysis of variance for the first 10 days of acquisition. In overall acquisition over the 10-day period the pigmented animals did not differ significantly from the albinos ($F(1,32) = 2.49$, $p > .05$), however both groups given differentially reinforced prior exposure performed significantly better than the control groups ($F(1, 32) = 16.38$, $p < .01$). The interaction between Rat

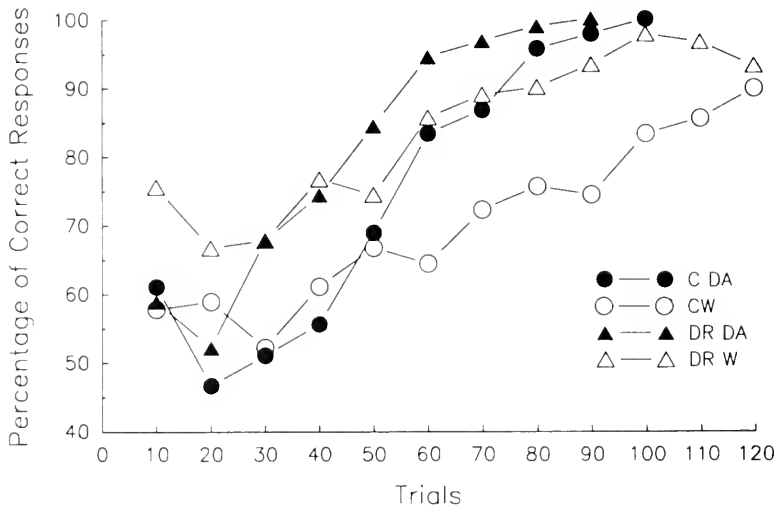


FIGURE 1. Mean percent correct responses for blocks of 10 discrimination trials for the four groups in the experiment (Control Dark Agouti, Control Wistar, Differentially Reinforced Dark Agouti and Differentially Reinforced Wistar).

Type and Condition was not significant. The days effect was significant ($F(9, 288) = 4.92, p < .01$). The Days \times Rat Type interaction was significant ($F(9, 288) = 4.92, p < .01$), because of the flatter learning curves of the albino groups, compared to the steeper curves of the DA groups (Figure 1). The Days \times Condition and the Days \times Condition \times Rat Type interactions were not significant. An epsilon factors for degrees of freedom adjustment was made for the days analysis. Thus, on this measure, although W and DA rats did not differ significantly in total number of correct responses, they did differ in rate of change of correct responses over the first 100 trials.

DISCUSSION

Both the pigmented DA and albino Wistar differentially reinforced prior exposure groups showed a significant enhancement of learning despite the fact that the negative cue (vanilla) had previously been found in the pilot study to be preferred to the positive (peppermint) cue.

Caza and Spear (1984) have commented that the effect of pairing an odour cue with positive reinforcement may simply reduce neophobia by making the odour less aversive in comparison to a novel

odour. When a preference test is used to examine the effect of pre-exposure to a single odour, a control condition (e.g., exposure to the odour without reinforcement) is necessary to account for the neophobia reducing effect. As we used a discrimination task rather than a preference test we did not include such a control condition. Any neophobic reaction in our control groups would only be present at the earliest stage of training. However, as is evident in Figure 1, on the first 20 trials one of the differentially reinforced groups (DRW) performed better than its control group and one (DRDA) did not perform any better than its control group. Superiority of each DR group over its control became more obvious as trials increased, when neophobia would no longer be present.

The enhancement effect of odour pre-exposure for the albino rats in this experiment was much stronger than that observed in the earlier visual-tactual exposure to shapes where a significant effect was evident only in the early stages of learning. In that study, brown rats given shape pre-exposure performed significantly better than their albino counterparts. On the odour task there was no such simple relationship. The extent of facilitation from DR exposure was the same for DA and Wistar rats, on both trials to criterion and correct response measures (neither Rat Type \times Condition interaction was significant). However on the correct response measure, there was a significant Days \times Rat Type interaction because of both Wistar groups' rates of acquisition being slower than that of the DA groups.

As the shape of learning curves was similar for the C and DR groups within each variety of rat, as evidenced by the absence of any interaction effect between Days and Conditions, the differences between the rat varieties appear to be related to aspects of the discrimination task which were common to both the control and experimental conditions. The pigmented rats made more errors in the early stages of learning and this showed particularly as an absence of enhancement of odour test performance on the first 20 trials for the brown DR group. This may well have been due to the brown rats showing a strong reaction when first introduced into the test apparatus even though it was very similar to the exposure apparatus. They were very reluctant to respond on the first two or three days of testing. They displayed freezing responses often refusing to leave the holding section of the discrimination apparatus for the stimulus area for several minutes. Even when DRDA rats were forced to stay in the stimulus compartment by lowering the dividing shield, they were reluctant to make a response and appeared to respond without attending to the odours. They would immediately return to the holding area often without retrieving the food reward, suggesting that they initially found the different test apparatus aversive. On the other hand, the albino rats appeared unaffected by the transfer to the test situation

and responded readily, taking many fewer minutes to complete 10 trials. Differences in neophobic or exploratory behaviour have been reported among various strains of rats (Harrington, 1971).

The slower rates of acquisition by the albinos over the later stages of learning led to the differences in trials to criterion between the two types of rat. It is unlikely that there are physiological differences related to odour detection in the two strains to account for the generally slower rate of acquisition by the albinos. Moulton and Beidler (1967) found no differences in nasal mucosae between albino and pigmented rats, and albino rats had a slightly lower threshold for odour detection. Beidler found no evidence that albino rats were more adversely affected by respiratory infection with corresponding partial anosmia. None of the subjects in our study displayed overt symptoms of respiratory infection. It should also be noted that the Wistars were more variable on trials to criterion measure (as shown by respective standard errors in Table 1).

The different performance patterns of albino and pigmented rats found with the odour task had also been evident in a two dimensional (visual) shape discrimination task and a tactual reduced visual task (Bell & Livesey, 1988). It appears that once the pigmented rats had adapted to the apparatus, they were better able to maintain discrimination performance with respect to the relevant cues. In the later stages of learning it was noted that, in both the odour and the visual tasks some of the albino rats, although performing at between 70-90 percent correct responses on one day, were not able to maintain criterion performance level (90%) over the required number of days. On some trials these animals appeared to be using irrelevant cues. In particular, the motor response involved (panel push) seemed to lead some of the albino rats to attempt to select the correct panel on the basis of the pressure required to open it. Two experimenters independently observed rats surreptitiously and gently pushing at the corner of one or both panels. If the panel gave easily, the rat would push it completely open. The same strategy had been observed in a previous study in tasks with reduced visual cues (Bell & Livesey, 1988). However, this tactic was irrelevant to the task as the pressure required to open the panels did not differ systematically and was certainly not related to which was the positive or negative odour stimulus. The strategy resulted only in the albino rats continuing to make errors. This kind of behaviour and accompanying erratic performance was much less evident in the brown rats.

This response strategy in the albinos appeared to be reduced by the effect of the differentially reinforced pre-exposure, which made the odour cues prepotent in the task. We, therefore, suspect that for the albino controls, the odour cues were not as potent and that the

nature of the panel push response predisposed them on some occasions to test the panels for ease of opening. In an experiment by Jennings and Keffer (1969), with a different type of response (running into the alley with the correct odour cue), albino and hooded rats did not differ in the learning of odour discriminations. Thus, it appears that albino rats may compensate for reduced visual capability by the use of other sensory information. In the context such as our discrimination task where it was assumed that the odour cues would be quite potent, to some animals, kinesthetic cues offered a conflicting source of possible (but incorrect) information.

With this experiment we have extended our reinforced pre-exposure paradigm to learning with odour cues. Differentially reinforced pre-exposure to odours significantly enhanced discrimination learning for both pigmented and albino rats when the exposure and test environments were very similar. This can be contrasted with the Lubow et al. (1976) finding that prior exposure to nonreinforced odour cues did not enhance discrimination performance when the environments were the same, but was facilitatory when the environments were quite different. We have previously explained these effects in terms of two different learning processes (Bell & Livesey, 1981). One involves learning of stimulus properties whereby particular properties defining a stimulus within the total stimulus input are isolated (Gibson, Walk, and Tighe, 1959). This is exemplified in Lubow et al.'s study and in our non-differentially reinforced prior exposure studies. The other process in which stimuli (cues) without relevance for an animal may acquire significance when associated with events that are of importance for its survival, e.g., food, we have described as learning of cue significance. It appears from a number of experiments that stimulus property learning transfers across different environments but that cue significance does not transfer in this way (Bell & Livesey, 1981). Our concept of cue-significance learning is related to other postulations involving sign tracking (e.g., Jenkins, Barrera, Ireland, & Woodside, 1978), and transfer of control (e.g., Thomas, 1985; Bolles, 1975).

We had expected that pre-exposure to odour cues would be more effective than that with the shape cues used previously. This was certainly the case for albino rats, who did not learn a great deal from the pre-exposure to the shape cues but did benefit considerably from the learning situation with the olfactory cues. The comparable albino DR group on the shape task took a mean of 146 trials to reach criterion (66 trials more than the odour DR group), while the control group took 154 trials (36.5 trials more than the odour group). For the brown rats, the DR group on the shape task reached criterion in 124 trials (56.3 more than the odour DR group), and the C group in 146 trials

(63.8 more than the odour C group). The magnitude of the facilitatory effect from DR pre-exposure for the pigmented rats thus appeared similar for the shape and odour pre-exposure.

While the odour task appeared to be learned more rapidly than the shape task, we had anticipated that the odour task with clearly distinct vanilla and peppermint cues would have been learnt more quickly than was the case in this experiment. However, the particular method that we used placed some constraints on the rate of learning. Furthermore, it is difficult to compare our results with other studies because often the authors did not give a trials-to-criterion measure or relevant procedural details such as the learning criterion. Experiments using the maze-learning procedure often yielded very rapid learning; with various odour cues, criterion was reached in 30-60 trials (Jennings & Keefer, 1969); in Ruddy (1980), with lemon/lime, vinegar/alcohol, clove/cinnamon cues, 30-40 trials to criterion but with the not very stringent criterion of 8/10 correct responses. In Kimble and Zack's (1967) study control animals learnt an anise/peppermint task in a mean of 81 trials.

While the present task was not learnt as quickly as some of the others reported, we did use a very stringent criterion of 9/10 correct responses over three consecutive days. Also the response component of our task (pushing open the positive cue panel) was probably more difficult than the maze type tasks and this appeared to be particularly so for the albino rats. According to Mackintosh (1983), most simultaneous discrimination tasks require only approach to or contact with the positive stimulus for the correct response, (e.g., maze tasks). Such responses may be largely a product of a classical contingency between the positive stimulus and reinforcement, similar to an autoshaped response. In our task the response involved appears to be more difficult. In none of our pre-exposed experiments was there perfect transfer from differentially reinforced exposure to the discrimination task (Bell & Livesey, 1977, 1981). The panel push response (with non-correction) required further learning before criterion level of performance was reached. For some of the albino rats, the response provided a particular difficulty as it appeared to lead to attention to an irrelevant cue—the pressure required to open the panel.

The albino rats were shown to learn more from odour pre-exposure than they had from pre-exposure to shape (visual/tactual) cues. This is in line with findings from other studies comparing learning with olfactory and visual or auditory cues (Nigrosh et al., 1975). However, the slower acquisition rate of the albinos compared with the pigmented animals has suggested that the response component of the task provided a particular difficulty. This again emphasizes that the relationship between discriminative cues and the motor requirement of a particular response for a particular subject must always be taken

into consideration when assessing the rate of learning (Bell & Livesey, 1985, 1988).

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THE RELATIONSHIP BETWEEN SOCIAL BEHAVIOR AND GENITAL SWELLING IN CAPTIVE FEMALE CHIMPANZEES: IMPLICATIONS FOR MANAGING CHIMPANZEE (*Pan troglodytes*) GROUPS

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ABSTRACT: This study was conducted as a portion of a project investigating relationships among reproductive cycling, aggression, and wounding in captive chimpanzees. Changes in behavior associated with the genital swelling of 11 adult female chimpanzees socially housed in four different groups were measured using 282 hours of data gathered within a 20-month period. The females' perineal swellings were rated daily using a five-point scale indicating level of tumescence. Behaviors recorded when the animals were detumescent were compared with behaviors when their sexual swellings were maximal. In addition to the subject's genital swelling rating, two factors, the male-to-female ratio in the groups and the presence or absence of a tumescent female other than the focal animal, were also included in the analysis. Multiple regression analysis revealed significant effects of each of the three factors. Significantly higher levels of sexual behavior and lower levels of submission were associated with the tumescent stage of cycling. Scores for affiliation, aggression, abnormal behavior, inactivity, locomoting, and being followed did not vary significantly with swelling phase. Group structure (male-to-female ratios) affected affiliation, locomoting, being followed, and aggression levels. Affiliation, submission, and locomoting were influenced by the presence of a tumescent female in the group. Proximity to other adult females increased during the tumescent stage of swelling, but proximity to adult males did not change. The group structure and whether or not a tumescent female was present affected various aspects of proximity to all age/sex classes of group members. Some findings from this study may be explained by the long-term stability of group membership in the colony studied, and implications for colony management are discussed.

INTRODUCTION

The studies of female chimpanzee (*Pan troglodytes*) behavioral changes associated with estrous cycling and ovulation have focused

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mainly on sexual behavior (Coe, Conolly, Kraemer, & Levine, 1979; Lemmon & Allen, 1978; Wallis, 1982; Yerkes & Elder, 1936). More recently, some investigators have measured influences on other behaviors (Goodall, 1986; Wallis & Lemmon, 1986; Wallis, 1986). These findings have been described in terms of female sexuality, behavioral changes associated with pregnancy, and the evolution of the chimpanzee mating system. The purpose of our study was to examine from an applied perspective, whether reproductive cycling, the presence of other cycling females, and group composition affected female behaviors and to determine whether such effects need be considered in the management of chimpanzee colonies.

The female chimpanzee's perineal region increases in size and turgidity as she approaches the time of ovulation. This genital swelling apparently attracts males by providing a visual cue for female reproductive status (Dixon, 1983 cited in Wallis, 1986; Graham, 1981). Rates of copulation, genital inspection, food sharing, and grooming are all affected by female chimpanzees' cycles (Harcourt, 1981; Lemmon & Allen, 1978; Wallis, 1986), as is the relative occurrence of male or female initiation of some of these social interactions (Wallis, 1986). Free-ranging females have been described as showing various levels of sociality, grooming, copulating, "nervousness," submission, and "assertiveness" at different points in their cycles (Goodall, 1986).

Goodall emphasized the strong influence of this factor by stating that "the presence or absence of cycling females is without doubt the single most significant factor in overall patterning of the chimpanzee community from year to year" (1986, p. 158). Females with a genital swelling may be in the company of many males as they travel and forage, but a female with no swelling is generally not near adult males (Goodall, 1986). The congregation of males around sexually receptive females sets up the circumstances for male-male competition for access to ovulating females, although in the wild this competition is not necessarily expressed by intermale aggression (Harcourt, 1981).

Since adult male chimpanzees form the cohesive unit around which free-ranging chimpanzee groups are organized, it is logical to establish multi-male groups of captive chimpanzees (Fitch, Mershalski, & Bloomsith, 1989). Such arrangements are also a practical means of allowing social housing for the large number of adult male chimpanzees in captivity, but there are advantages and disadvantages for the group members (see Fitch et al., 1989 discussion). In our colony, an analysis of veterinary wounding records indicated an increase in the total number of wounds inflicted in multimale-multi-female social groups when at least one of the group's females displayed a maximal genital swelling (Alford, Bloomsith, Keeling, & Beck, 1990; Lambeth, Bloomsith, & Alford, 1990). This wounding is

probably an outcome of male-male competition and is certainly a problem for the colony manager, although it is acknowledged that some aggression among captive chimpanzees is "normal" and to be expected even among well-socialized groups.

This study was the first in a group of studies designed to identify and characterize factors influencing captive chimpanzee agonism. A second study will measure levels of agonism when female group members are at different points in their reproductive cycles (Bloomsith, Lambeth, & Alford, accepted) and a third study will test a strategy for reducing the agonism potentially associated with the cycling of females. Although the spatial constraints of captivity may influence the effects of female cycling on social behavior, some influences on social interactions would still be predicted from the strength of the findings with free-ranging subjects. Based on those findings, we expected to find in the present study that changes in female affiliation, agonism, sexual behavior, and proximity to adult males would be associated with changes in genital swelling. This information could then be used to identify the female's role in the increase in wounding associated with cycling females, as documented in our colony records.

METHODS

Animals

The animals were 11 sexually mature, nongravid, female chimpanzees (*Pan troglodytes*) socially housed with adult males, adult females, and immature chimpanzees in four different groups. Social groups of 2 to 4 adult males, 2 to 5 adult females, and 2 to 5 immatures were housed in enriched outdoor corrals (22 m in diameter) with access to additional indoor quarters. During observation periods focal animals and their groups were limited to the outdoor portion of their enclosures. The animals' ages ranged from 10 to 26 years old.

Data Collection

A total of 282 hours of data were collected between May 1988 and January 1990, with a range of 18 to 30 hours of data collected per chimpanzee. Each chimpanzee was observed between one and three times weekly at various times throughout the day. Data collection consisted of 15-min focal animal observations (Altmann, 1974) with data recorded at 10-s intervals.

The behavioral categories were affiliative interactions (rest in contact, move in contact, groom, play initiation, play, embrace), aggressive interactions (threat, brusque rush, attack), submissive inter-

actions (avoid, crouch/bob, pant-grunt, bared-teeth scream, present in an agonistic context, flee), sexual behavior (receive genital exploration, present in a sexual context, receive mount/thrust, move away from a mounting male, explore genitals of another), and other behaviors (inactive, locomote, abnormal, being followed by another animal, and "other"). (See Appendix for operational definitions.)

Proximity of the focal animal to her group members was also recorded during the same intersample interval. The identity of each chimpanzee in the proximity of the focal animal was recorded. Proximity was defined as two individuals being within 1 m of each other. The mean percentage of agreement by observers across all behavioral categories was 92%, as measured monthly, and the mean percentage of agreement on proximity scores by four observers was 93%.

The degree of swelling of the sexual skin of each female was recorded daily by one of two trained members of the caregiving staff. A 5-point scale (with ratings of 0 to 4) was used to rate the swellings (Graham, 1981). Behavioral data collected on days when the genital swelling was rated as a "2" were excluded to clearly differentiate the two ends of the scale, and the remaining information was separated into two categories as described below. The interobserver reliability on the swelling ratings was 84% agreement.

Data Preparation and Analysis

The scan-sampling behavioral data were summarized for each session to estimate the percentage of time the chimpanzee was engaged in each behavior. This information was then compiled and grouped across all animals by the five stages of the female's estrous cycle. Data were then combined into two categories, the detumescent condition (ratings of 0 or 1) and the tumescent condition (ratings of 3 or 4).

The scan-sampling proximity data were summarized by adding the number of points at which the focal animal was within 1 m of an adult male, an adult female, or an immature group member during each observation session. This information was then compiled across focal animals by the genital swelling phase, as described above.

Because of their potential influence on behavior, two other factors were also analyzed: the presence of another tumescent female and the adult male-to-female ratio in the animal's social group. There was another tumescent female present (other than the focal animal) during approximately 35% of the observations. During 90% of the data collection sessions, the male-to-female ratio was either 1:1 (three adult males and three adult females) or 1:2.5 (two adult males and five adult females). The remaining 10% of the data were collected under a variety of group compositions. Because these data were too few for analysis, they were excluded.

Data were analyzed by applying multiple regression techniques, which in some cases were followed by an analysis of variance test applied to residuals. All tests were two-tailed, and an alpha of 0.05 was used to determine significance. Several transformations on the original data led to no improvement in the information derived from the data.

RESULTS

A multiple regression measuring the effects of three factors (genital swelling, presence of a tumescent female, and group composition) was computed for each of the eight dependent measures of interest. Each factor significantly affected at least one dependent measure (see Table 1 for individual values). When tumescent, the focal animals showed a statistically significant increase in sexual behavior. Their level of submissive behavior was reduced, but the reduction did not satisfy the alpha level set. The presence of a nonfocal tumescent fe-

TABLE 1
Statistical Relationships Between the Three Factors of Interest and the Eight Dependent Measures.

<i>Dependent Measure</i>	<i>Factor</i>		
	<i>Phase of Genital Swelling</i>	<i>Presence/Absence of Nonfocal Tumescent Female</i>	<i>Group Structure</i>
Aggression	NS	NS	NS ²
Submission	-.06; NS ¹	NS ²	NS
Affiliation	NS	.04; $p = .003$.19; $p < .001$
Sexual Behavior	.13; $p < .001$	NS	NS
Abnormal Behavior	NS	NS	NS
Inactivity	NS	NS	NS
Being Followed By			
Another	NS	NS	-.07; $p = .025$
Locomotion	NS	-.03; $p = .006$	-.10; $p < .002$

A three-factor multiple regression was computed for each dependent measure. The standard coefficient and the associated p value for each factor is reported.

¹ $p = .06$

²A two-factor multiple regression was computed for each dependent measure which excluded the genital swelling factor. Subsequently the residuals were analyzed by ANOVA to measure an effect of genital swelling. Two additional dependent variables, submission ($-.07$; $p = .02$) and aggression ($.06$; $p = .04$), were determined to be significantly related to the presence of a nonfocal tumescent female and group structure respectively. Relationships to genital swelling phase were unchanged.

male reduced levels of submission and locomotion among the chimpanzees and increased their affiliation. The focal animals living in a group with a male-to-female ratio of 1:2.5 showed more affiliation, showed less locomotion, and were followed less often than those living in a 1:1 group structure. Focal animals in the 1:2.5 group structure engaged in approximately three times as many scans with affiliation as those in the 1:1 structure (20% versus 7% of the data scans). Approximately three-quarters of this affiliative behavior recorded in each of the group structures was social grooming.

Due to concern over reduced statistical power from including three factors in the multiple regressions on infrequently occurring dependent measures, additional analyses were performed. Multiple regressions were computed to remove the variance associated with group structure and other tumescent females, and the residuals were then tested for an effect of genital swelling using an ANOVA. The multiple regressions with only these two factors revealed a significant relationship to two other dependent measures: the 1:2.5 group composition was associated with more aggression than the 1:1 group structure; the incidence of submissive behavior was significantly higher when there was no other tumescent female in the group. The ANOVA results for effects of genital swelling were identical to those found using the three-factor multiple regression.

The patterns of association with other individuals in the group were examined by summarizing and analyzing the proximity data in three ways. First, the absolute values for the incidence of proximity to group members were calculated. Multiple regression of absolute proximity values for genital swelling phase, the presence of a tumescent female in the focal animal's group, and group composition showed significant effects (Table 2).

When tumescent, animals had higher scores of proximity to other adult females; there was no change in their proximity to adult males or to immatures. The presence of a tumescent female in the focal animal's group also increased the score for proximity to other adult females. Chimpanzees in the group with a 1:2.5 male-to-female ratio were near other group members more than those in a 1:1 male-to-female ratio. Higher levels of proximity to adult females and to immatures were measured, but there was no difference in proximity to adult males.

The second treatment of the proximity data was adjusted for the number of available partners by dividing the absolute proximity values by the numbers of group members in the appropriate age/sex class. These adjusted proximity values were then analyzed by a multiple regression. Genital swelling had no effect on any of the adjusted proximity scores. The presence of a tumescent female in the focal animal's group increased her proximity both to adult males and to adult

TABLE 2
Statistical Relationships Between the Three Factors of Interest
and the Proximity Measures.

	<i>Factor</i>		
	<i>Phase of Genital Swelling</i>	<i>Presence/Absence of Nonfocal Tumescence Female</i>	<i>Group Structure</i>
<i>Absolute Proximity Scores:</i>			
To Adult Males	NS	NS	NS
To Adult Females	.08; $p = .01$.10; $p = .002$.13; $p < .001$
To Immatures	NS	NS	.23; $p < .001$
To All Group Members Combined	.06; $p = .04$.09; $p = .007$.22; $p < .001$
<i>Proximity Scores Adjusted for Number of Partners:</i>			
Mean to Each Adult Male	NS	.06; $p = .05$.08; $p = .01$
Mean to Each Adult Female	NS	.07; $p = .04$.06; NS ¹
Mean to Each Immature	NS	NS	.14; $p < .001$
Mean to Each Group Member	NS	.07; $p = .04$.17; $p < .001$
<i>Percentage of Proximity to Each Age/Sex Class:</i>			
To Adult Males	NS	-.07; $p = .05$	NS
To Adult Females	NS	.11; $p < .001$	NS
To Immatures	NS	NS	.14; $p < .001$

A three-factor multiple regression was computed for each dependent measure. The standard coefficient and the associated p value is reported.

¹ $p = .06$

females. These adjusted proximity scores for all age/sex classes of group members were higher in the group with a 1:2.5 composition.

The third summary of the proximity data was made to calculate the percentage of the proximity scores that were directed toward each of the three age/sex classes previously identified. Multiple regressions for each age/sex class revealed that genital swelling had no effect on

the percentage of the proximity scores associated with age/sex class. The presence of a nonfocal tumescent female significantly increased the percentage of proximity to adult females and to adult males, but had no effect on the proximity to immature group members. Only the percentage of total proximity to immature group members was affected by group composition, with a greater level of proximity in the 1:1 groups.

The copulation rate was calculated for all focal animals combined. In 118.5 hours of observation when females were at the low stage of swelling, one copulation was observed, giving a rate of .008 copulations per hour. When females were at the high stage of swelling, five copulations were observed during 134.5 hours, giving an hourly rate of .04. (As mentioned in Methods, data from females with a tumescence rating of 2 [29 hours] were not analyzed.)

DISCUSSION

In this study, the behavior of adult female chimpanzees was influenced by their own reproductive cycling, by the presence of other cycling females in their social groups, and by the ratio of adult males to adult females in their social groups. These factors affected different aspects of female behavior. Consistent with previous studies (Goodall, 1986; Wallis, 1986), the incidence of sexual behavior rose during the tumescent stages of females' cycles. Genital explorations of the focal females doubled between the detumescent and tumescent stages and was the most frequent sexual interaction. Copulations were infrequent, with only six observed during the 282 hours of observation. This is much lower than copulation rates reported in the wild (Goodall, 1986; Tutin, 1979; Tutin & McGinnis, 1981) or in other captive populations (Coe et al., 1979).

In addition, females with a maximal genital swelling showed a tendency toward exhibiting less submissive behavior than those in a detumescent stage of their cycle. The reduction in submissive behavior could result from at least two situations. Fewer aggressive actions may be directed toward the females during tumescent stages of their cycles, therefore eliciting fewer submissive responses, or females may respond to the same social situations differentially, based upon their cycling status. Which situation best explains these findings cannot be discerned from these data because the collection technique did not incorporate sequences of behavior. However, Goodall stated that female chimpanzees in Gombe became "more assertive during maximal swelling" (1986, p. 483). Unseen and submissive females that normally remained at the perimeters of the social group would become visible and approach dominant males, sometimes begging for food

when cycling. Similarly, Nishida stated that "estrus seems to eliminate an adult female's shyness and makes her bold and aggressive" (1979, p. 103). Findings from the current study indicate that a similar phenomenon may be manifested in captive females.

No behaviors other than sex and submission were affected by genital swelling phase. It should be noted that rating genital swellings is not equivalent to detailed hormonal information, which would more closely represent the phase in each female's reproductive cycle. It is possible, for example, that some of these females' cycles were anovulatory. The methods used have the shortcoming of not accounting for such events.

Based upon our previous finding of increases in the number of wounds inflicted in multimale-multifemale groups when there was a female with a tumescent swelling present, one might expect that adult females would be involved in more aggressive episodes themselves. Our findings contradict that hypothesis. Further examination of our wounding records after this study was completed have indicated that the effect of tumescent females on rates of wounding has been eliminated in recent years in some groups with long-term stability (Alford et al., 1990; Lambeth et al., 1990). Unfortunately, since data for the current study were collected only on groups that had been stable over a long period of time, we cannot discern whether females may have been directly involved in the increase in wounding measured in past years.

The presence or absence of a tumescent female group member has an indirect impact on the behavior of other female group members. Females engage in more affiliation, less submission, and less locomoting when a group member has a tumescent swelling. These changes seem to be generally consistent with a more relaxed, less socially tense atmosphere when at least one other female group member is displaying a maximal swelling. There is no evidence, for example, that adult males redirect aggression from tumescent females toward other (nontumescent) females in the group. It is important to note that this finding relates only to adult females. Members of other age/sex classes may respond differently.

Finally, the adult composition of the groups also seems to have an impact on several behaviors that could be related to the level of social tension in the group. These results should be viewed with caution however, because only one of the groups studied had a group composition of 1:2.5. In the group with a 1:2.5 male-to-female ratio, the females were more affiliative, spent less time locomoting around the enclosure, and were also followed by another animal less often. However, these females also engaged in more aggression. Perhaps two adult males could not control female aggression as effectively as can males in a 1:1 group structure. One possible explanation for the

positive relationship between levels of affiliation and of aggression is that social grooming (the behavior that composed most of the category of affiliative behavior) may be a tension-reducing, reconciliatory behavior that may increase in association with agonistic episodes (Nieuwenhuijsen & de Waal, 1982). In other words, perhaps these females fought more, so they reconciled (e.g., groomed) more.

Most unexpectedly, affiliation and the proximity of females to adult males were not affected by changes in genital swelling. Females did not show an increase in the number of times they were near males, nor was there any evidence for a bias toward a greater percentage of proximate activity to involve males at times of maximal swelling. Contrary findings would have been predicted based on relevant literature that describes increased prosocial interactions (Coe et al., 1979; Harcourt, 1981), particularly male-initiated interactions, as females' cycles progress toward ovulation (van Lawick Goodall 1968; Goodall 1986; Wallis, 1986). The group structure had various effects on proximity to other group members, as did the presence of a tumescent female.

The extremely low rate of sexual activity, the lack of effect of reproductive cycling on affiliative behavior, and the lack of an increase in proximity to males during tumescent stages of cycling are in contrast to other published findings. Each of these results may be influenced by a particular feature of the chimpanzee colony studied, and so may not be generalizable. This colony has shown a decrement in reproductive performance (e.g., number of conceptions) in the last few years, and a subjectively noticed reduction in sexual behavior. We hypothesize that this effect may be due to long periods of stability in group membership (in most cases at least 7 years when the data were collected) and a resulting "boredom" with available sexual partners. A similar effect of familiarity on captive chimpanzee sexual interactions has been documented (Allen, 1981; Coe et al., 1979). An objective study of this phenomenon in The University of Texas colony is planned, but the effect appears to be so strong that we feel confident in hypothesizing an influence on intragroup interactions. While the generalizability of these findings may be somewhat constrained because of the influence of group stability, this information certainly can be applied to other settings in which long-term group stability is maintained. Larger social groups of chimpanzees are becoming more common as laboratories and zoos are attempting to improve the social conditions for their chimpanzee residents. This information will be useful to apply as those groups remain intact over many years.

The current results indicate that chimpanzee behavioral management problems may change as colonies are housed in stable groups over long periods of time (see Nieuwenhuijsen & de Waal, 1982 for evidence of decreasing aggression over time). For example, reduced

breeding performance may become a problem rather than agonism and wounding problems resulting from intermale competition for females. In the future, we will more fully examine these issues by studying the effects of reproductive cycling on wounding and on group measures of agonism, and by examining the effect of familiarity on sexual behavior.

From a behavioral management perspective, these findings indicate that, in our colony with multimale chimpanzee groups, changes in the genital swellings of females do not seem to lead to any problems that demand the attention of colony managers. Our original goal of documenting the females' role in increased group agonism during certain phases of their cycle has been changed, as further analysis has shown that this agonism is eliminated with long-term stability in group membership (Bloomsmith, et al., accepted). There is probably little a colony manager can do to arrange groups so that at least one tumescent female is present, but this may have beneficial effects on other group females. These data indicate that group structure can be manipulated by colony managers, perhaps to influence levels of female affiliation or aggression. Since these behaviors varied together, it may be that groups with particular structures require more careful monitoring for problems with aggression. If a colony manager wanted to encourage a particular female's expression of social behavior, a group containing more females than males may be an appropriate choice. On the other hand, if female aggression is really a problem, having an equal number of adult males as adult females may help to reduce the problem. Certainly, stability in group membership should be encouraged from the point of view of creating a more peaceful and safe environment for chimpanzees, as long as one realizes that problems with breeding performance may then have to be addressed.

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APPENDIX: Operational Definitions of Behaviors Analyzed

Affiliative Behavior

Play Initiation—Includes a variety of behaviors, such as run-past, slapping the ground or rolling in front of another individual, that culminate in a play bout. Usually accompanied by a play face.

Social Play—Includes rough-and-tumble play (fast-paced, vigorous locomotion, wrestling, hitting, pulling, chasing, biting, etc.) and quiet play (slower-paced, gentle tickling, finger and toe manipulating, etc.). Never accompanied by piloerection; may be accompanied by play-face and/or laughing.

Embrace—Usually ventro-ventral contact of two individuals. One or both may have arms around the other. Hands are *relaxed* (i.e., not clutching fur of the other). In some instances an animal may embrace another from the side or the back.

Rest in Contact—Physical contact with another animal that is not recorded under a different behavioral category. Animals are not locomoting and are touching one another.

Move in Contact—Physical contact with another animal that is not recorded under a different behavioral category. Animals are locomoting and are touching. Carrying an infant is excluded.

Social Groom—Picking through hair or at skin and removing debris with hands and/or mouth. Does not include pulling hair out. Focal animal may direct or receive this, or it may be mutual.

Agonistic Behavior

Avoid—Focal animal moves away as another approaches or moves out of the path of another. May involve a flinching movement (slight ducking of the head or head and shoulders).

Crouch/Bob—Focal animal lowers its body by flexing its arms and legs until it is in a horizontal position touching or nearly touching the substrate. May tuck its head between drawn up shoulders or press its face against the ground. Vertical, repeated movement of the head or head and shoulders in an “up-and-down” pattern.

Pant Grunt—Rapid, rhythmic series of grunts or barks directed toward another. Sometimes accompanied by crouching or bobbing (after Bygott, 1979).

Bared Teeth Scream—Mouth widely opened, lips fully retracted from teeth and gums with high-pitched, intense intermittent screams (after van Hooff, 1974).

Flee—Focal animal moves away from another at full speed. Often accompanied by bared teeth screaming (after van Hooff, 1974).

Threat—Includes head tip (a slight, upward jerking movement of

the chin), arm-raising, arm-waving, wrist-shaking, and lunging toward another animal.

Brusque Rush—Locomotion during which animal moves toward another at full speed often with piloerection (often as a component of a display). Can be a male or female exhibiting this.

Attack—Aggressive interaction involving physical contact. Focal animal hits, tugs, grabs, bites, stomps on, rolls, or repels the other animal involved (after Bygott, 1979).

Sexual Behavior

Receive Genital Exploration—Focal animal's genitals are visually, orally, or manually inspected by another.

Present—Focal animal's posture varies from slight flexion of the arms or turning rump toward another to an extreme crouch with all four limbs folded under it so it is close to the ground. (The context of the behavior is judged to distinguish sexual from agonistic contexts.)

Receive Mount/Thrust—Female remains stationary while a male is mounting her.

Move Away—Female moves away from a male that has "solicited" toward her (sits facing her with thighs rotated laterally, generally has an erection, and exhibits pelvic thrusting); has attempted a genital explore or has attempted a mount.

Genital Explore—Focal animal visually, orally, or manually inspects another animal's anogenital region.

Miscellaneous Behaviors

Inactive—Focal animal is immobile, not engaging in any activity. Includes lying down, leaning, and reclining. The animal appears to be sleeping.

Locomote—Focal animal's whole body is moving through space. Includes walking, climbing, brachiating, etc. If the focal animal is contacting another chimpanzee while locomoting, "move in contact" is recorded rather than locomote.

Abnormal—Includes coprophagy, feces spreading, urophagy, hair plucking, regurgitating, bizarre posturing, self-slapping, rocking, and idiosyncratic stereotypies (Walsh, Bramblett, & Alford, 1982).

Receive Follow—Another animal follows the focal subject.

Other—Behavior not included under any other category in the ethogram.

BOOK REVIEWS

Spontaneous alternation behavior edited by W. N. Dember & C. L. Richman. Springer-Verlag, New York, 1990, XII + 211 pp.

If an adult rat is placed in the start stem of a T-maze, allowed a choice of one of the arms, and then placed immediately back into the maze and allowed a second choice, about 80% of the rat's second choices will be the arm opposite to that entered in the first trial. This is named *spontaneous alternation behavior*, or SAB, and was first observed by Hunter (1914) in a study on discrimination learning. Why would comparative psychologists be interested in such a simple phenomenon?

I started my reading of Dember & Richman's (D&R) book with some expectations I usually experience when reading a collection of chapters, i.e., that heterogeneity of topics and styles will prevail, that it will be hard to find a common theme, and that there will be a lot of "unpublished results" which may not be appropriate for publication in major journals. I was glad to discover that I had been wrong. D&R had put together a very coherent set of chapters which does more than merely review the literature; it conveys a sense of accomplishment uncommon in the animal learning and behavior field. The authors have successfully avoided the further-research-is-necessary cliché, to concentrate on making sense of the impressive amount of information that has been obtained about SAB after several decades of research.

The historical overview presented by W. N. Dember reminds us of some important connections between the early literature on SAB and learning theory. SAB was initially conceptualized in terms of an *exploratory tendency* that would presumably drive rats toward novel places. It was Hull's notion of *reactive inhibition* what shifted attention from the environment to the animal's response. Reactive inhibition was conceptualized as an aversive, temporary state induced by the occurrence of a particular response; within Hull's theory, reactive inhibition was designed to account for some extinction phenomena, such as spontaneous recovery, but its relevance to SAB was obvious. Some early data on the dependence of SAB on relatively short inter-trial intervals seemed to confirm the role of reactive inhibition because this aversive state was thought to spontaneously decay in time. SAB entered therefore the *place vs. response* controversy that dominated the field of animal learning during the 1950s. The crucial ex-

periments were those in which the maze was reoriented 180° between the first and second trials. They revealed that intra- and extra-maze stimuli are far more important determinants of SAB than response-produced stimuli; the story is fully described in Chapter 2, also by Dember. Drawing mostly from the research of Douglas and his associates, Dember concludes that odor trails are the most important intra-maze cues determining SAB, and that the direction of movement relative to cues in the room where training takes place is the most important extra-maze cue for SAB. These two sources account for virtually all the alternation behavior of rats in typical laboratory situations.

The third chapter by R. N. Hughes deals with the interspecies generality of SAB and turn alternation, a related phenomenon—at least at the behavioral level—which seems particularly prominent in invertebrates. One interesting outcome of this review is the limited species generality of SAB: it has not been found in a number of invertebrates, with the possible exception of some cockroach species, in teleost fish, in turtles, or in domestic chicks. There is some evidence of SAB in marsupials, lagomorphs, rodents (in addition to rats), and carnivores. Unfortunately, very little has been done in these species beyond the basic demonstration of SAB. What do we want from a comparative study of SAB? We certainly do not want a survey of SAB in hundreds or thousands of species, but rather a systematic research program with a few carefully selected species which may give us an idea of the generality of the processes involved in the SAB observed in rats. The book so clearly illustrates the dependence of SAB on procedural aspects that it would seem naive to think that we can treat SAB as a morphological trait that is or is not present in a particular species.

SAB was discovered in the course of discrimination experiments and therefore it seems appropriate to ask for the potential relation between these two phenomena. C. L. Richman takes over this task in Chapter 4, pointing out the connections between SAB and such notions as *selective attention*, *response competition*, and *drive level*. Although it may appear on a first approximation that SAB may interfere (or enhance, depending on the training conditions) with discrimination learning, the relation is not so clear upon closer examination. SAB seems to depend on conditions which are not typically found in learning experiments. For example, food deprivation disrupts SAB and it is, of course, an omnipresent manipulation in learning experiments in which food is used as a reinforcer. Indeed, following Estes (1958), Richman suggests that food deprivation may increase acquisition rate “by eliminating an animal’s initial tendency to alternate” (p. 62). It may be the case that SAB is not so influential a factor in discrimination learning, as compared to other sequential

effects, such as position habits, as a number of experiments seem to suggest (e.g., Papini, Mustaca, & Affanni, 1985).

The next two chapters review the neurobiological (Chapter 5 by R. J. Douglas) and neurochemical (Chapter 6 by L. Kokkinidis) correlates of SAB. The neurobiological research reviewed by Douglas points to two sets of structures within the brain. First, the *hippocampal system* involving the entorhinal cortex, the subiculum, the hippocampus, the dentate gyrus, the fimbria and fornix, and the septal region. Douglas develops a parallel between the effects of hippocampal lesions in humans and rats, and suggests that when a lesion in a particular structure in the rat's brain abolishes SAB, a lesion in an analogous structure in the human brain will disrupt short-term memory. The second set of structures involves the *vestibular system*, including the labyrinth in the internal ear, the vestibular nerves and nuclei, the cerebellum, and the corpus striatum. Lesions in these areas significantly disrupt SAB, and may sometimes completely abolish it. Kokkinidis' chapter treats SAB as an example of the more general phenomenon of habituation, and suggests that drugs that disrupt habituation should also decrease alternation behavior. Anticholinergic drugs, such as *scopolamine* and *atropine*, reduced SAB levels to chance, whereas *amphetamine*, which blocks the reuptake of norepinephrine, eliminates SAB and induces perseverative movements.

The ontogeny of SAB in the rat was described in Chapter 7 by N. E. Spear and J. S. Miller. As they point out, SAB increases as a function of age in the rat, as well as in other species such as the Guinea pig, a precocial rodent with an almost complete development of the nervous system at birth. The central question that Spear and Miller try to answer is "why does the developing animal increase its probability of alternation?" After rejecting some alternatives (i.e., that infants alternate less than adults because they are less curious and less active), they describe the contribution of *emotional reactions to novelty*, *length of stimulus exposure*, and *forgetting rate*. For example, 16-day old rats, which would not normally alternate, may show adult levels of SAB if odors from their home cage are present during the test. Apparently, these familiar odors eliminate competing responses elicited by the experience of being isolated from the nest area. Additionally, and at least in the rat, some structures which are known to be important for SAB to appear in the adult, develop gradually during the initial weeks of life. For example, a unilateral lesion to the hippocampus, which produces no effect on SAB if performed in an adult, disrupts SAB in the adult animal if performed between 12 and 31 days of age.

The final chapter by R. J. Douglas reviews some personal experiences accumulated over years of SAB research, and is meant as "ad-

vice from a veteran." The chapter contains potentially useful information for someone new to these problems and it is very enjoyable reading. I found most of the advice to be sound and intuitively useful, although I am uncertain about Douglas' recipe for dealing with poor alternators: simply "dump them" (p. 149).

This book is recommended for those interested in animal learning and behavioral neuroscience, and perhaps may be a useful guide in graduate seminars focusing on a single issue. I found minor problems when in several chapters an attempt is made to relate SAB to foraging research; statements such as the "obvious survival value of SAB" (p. 39) clearly add only confusion both about the explanation of SAB and about the nature of the concept of adaptation. It is also not clear to me why it would be optimal for the animals to alternate; seeking novelty is not probably a "goal" in itself, in an evolutionary sense, and, in fact, alternation (and win-shift) may be more related to resource depletion than to other aspects of the environment (Kamil, 1978). In any case, the authors are to be congratulated on an excellent book which illustrates how far comparative psychologists venture when pursuing the understanding of a behavioral phenomenon.

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Cognitive ethology: The minds of other animals, edited by Carolyn A. Ristau. Lawrence Erlbaum Associates, Hillsdale, NJ, U.S.A., 1991, XX + 332 pp.

When we study animals either in their natural environment or in the laboratory, what does their behavior tell us about their mental

functioning? What can be inferred from behavioral data about their mental life? How should we approach and study consciousness and mental states of animals? Should we engage in such an enterprise at all? These problems, that have been matters of increasing debate and controversy for the last two decades or so, are at the very heart of Carolyn Ristau's book. The volume is dedicated to Donald Griffin and presents ideas and researches that have been inspired by his work. However, it is not just a collection of contributions supporting Griffin's ideas, but rather a lively array of different views, representative of a developing new field: cognitive ethology. The papers originate from a symposium on animal cognition held at the *Animal Behavior Society* meeting in June 1987.

The book includes two sections. The three chapters in Part 1 are concerned with theoretical perspectives and basic assumptions in cognitive ethology. The ten chapters in Part 2 present experimental evidence from both the laboratory and the field. However, theoretical aspects emerge continuously in the second part.

Donald Griffin begins Part 1 of the volume by outlining the main concerns of cognitive ethology. He suggests that animals might well have simple thoughts about things that matter to them. His working definition of consciousness assumes the presence of internal representations and simple beliefs and desires about objects and events; it does not necessarily include self-awareness and thinking about the process of thinking itself. Griffin explores some lines of evidence for the presence of consciousness and considers possible functions consciousness might serve. Cognitive ethology, and in general the study of animal cognition, he argues, "should certainly include, but not be limited to, information processing in animal brains."

The ethologist Colin Beer traces the historical and conceptual evolution of philosophical ideas central to cognitive ethology, providing a summary of so called "folk psychology" and other views in the philosophy of mind bearing upon the study of animal minds. Finally, the philosophical foundations of the intentional accounts of behavior, i.e., explanations based on mental states like beliefs and desires, are examined by the philosopher Jonathan Bennett. He develops the belief-desire-behavior approach to include an emphasis on the context and environment.

Different aspects of animal cognition are discussed by several contributors in Part 2. Ristau describes her field work on the injury-feigning behavior of plovers as well as other antipredator acts which suggest considerable cognitive ability. Gordon Burghardt focuses on reptile cognition and examines the death feigning of hognose snakes in the laboratory. Both Ristau and Burghardt explore the advantages and disadvantages of applying a belief/desire approach in research on animal behavior.

Communicative behavior is an interesting subject for studying the minds of nonhuman animals, and provides a potential window into problems of intentionality. Peter Marler, Stephen Karakashian, and Marcel Gyger describe their experiments on the effects of different audiences on the communication of chickens. The impact of social context on the production of signals with external referents like danger and food is of particular interest if one considers the possibility that animals may be intending to communicate, as opposed to merely emitting vocalizations in the presence of certain classes of eliciting stimuli. The focus is on one limited aspect of intentionality, namely the desire to communicate. The possibility for deception in animal communication is investigated by Dorothy Cheney and Robert Seyfarth, who discuss deceptive behavior of vervet monkeys and other species. They note that not all animal communication provides accurate and reliable information to recipients, but some signals provide others with false information (their functional definition of deception). The authors examine factors constraining the ability of animals to deceive each other. W. John Smith discusses critically the work by Marler and his colleagues and examines, in more general terms, the messages and meanings of animal signals, the nature and limitation of playback experiments, and the conclusions to be drawn from these. Finally, Irene Pepperberg advocates the usefulness of artificial communication systems in investigating cognitive and communicative abilities of animals, and describes her work on a parrot.

Alison Jolly reviews laboratory and field studies of primate behaviors that suggest consciousness, discussing instances of self-recognition, planning, symbolic behavior, and deception in chimpanzees.

Sonja Yoerg and Alan Kamil outline the limits of cognitive ethology, and argue that its definition as put forward by Griffin is "impractical and unproductive," because it focuses on unobservable conscious mental events. They claim that current cognitive ethology is virtually atheoretical and therefore no meaningful predictions can be made; furthermore, it is almost untouched by recent developments of human and animal cognitive psychology. They suggest that cognitive ethology should comprise the best of cognitive science and the best of ethology.

George Michel, a developmental psychologist, argues against "folk psychological" concepts by considering difficulties in their application to developmental psychology.

Finally, Ristau provides an overview of the book together with some critical comments about the papers and the state of the art. It turns out that the study of other minds is difficult and problematic for a number of reasons. More empirical data are necessary, as well as caution in their interpretation. However, entertaining possibilities of consciousness or thinking in animals led to the design of experiments

not otherwise likely to be undertaken. I fully agree with this statement and would extend it to the field of animal cognitive psychology. At least, the picture of animal behavior that has emerged in recent years from both cognitive ethology and animal cognition is by far more interesting, intriguing and complex than previously imagined.

As a whole, the book is extremely interesting and up to date, in that it provides a complete overview of current perspectives in its field. In my opinion, it is a stimulating source of ideas for new research. Certainly comparative and experimental psychologists, ethologists, and cognitive scientists can all profit from reading it.

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